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Effects of insufficient chilling on budburst and growth of six temperate forest tree species in Ontario

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Abstract

Insufficient winter chilling related to rising temperatures has raised questions about its potential effects on budburst timing (growth initiation) and subsequent tree growth. We quantified budburst timing and growth of seedlings of six Ontario temperate forest tree species after exposure to different levels of winter chilling using controlled forcing experiments. Based on chilling–forcing relationships, chilling requirements for the species tested ranged from 1000 to 1500 weighted chilling hours. Our findings showed that the species' chilling needs ranked from highest to lowest were yellow birch (*Betula alleghaniensis*), eastern larch (*Larix laricina*), eastern white pine (*Pinus strobus*), red pine (*Pinus resinosa*), red spruce (*Picea rubens*), and eastern white cedar (*Thuja occidentalis*). Species that needed more chilling to release dormancy generally required less cumulative forcing for budburst. The variations in chilling–forcing relationships among species suggest that they would respond differently to temperature changes, resulting in year to year variation in their relative phenology. Insufficient chilling increased cumulative forcing needed for budburst but only extreme chilling deficiency (< 700 weighted chilling hours) caused abnormal budburst and growth, including reduced leaf and shoot expansion, early and erratic budburst in lower branches and stems, and even lack of budburst after 7 months in optimal growing conditions. Overall, our results suggest that based on climate warming projected for this century, insufficient winter chilling is not likely to occur in Ontario temperate forests in the foreseeable future.

Keywords Chilling requirement · Forcing temperature · Climate warming · Winter dormancy · Spring bud phenology

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Introduction

Spring budburst starts the annual growth cycle, influencing tree growth, competitiveness, and adaptation, as well as species distribution (Chuine and Beaubien 2001), forest composition (Roberts et al. 2015), carbon sequestration, and forest productivity (Richardson et al. 2012). In boreal and temperate climates, spring phenology is controlled primarily by temperature: winter chilling under cool temperatures drives dormancy release (Cannell and Smith 1983; Hänninen 1990; Polgar and Primack 2011) and spring forcing at warm temperatures drives budburst (Hänninen 1990; Polgar and Primack 2011). Climate warming increases spring forcing and shortens the time to budburst, assuming sufficient winter chilling has occurred (Heide 1993; Chmielewski and Rötzer 2001; Schwartz et al. 2006; Morin et al. 2009; Beaubien and Hamann 2011; Chen et al. 2018). However, climate warming effects on winter chilling vary in space and time (Zhang et al. 2007; Polgar and Primack 2011; Fu et al. 2015a, b; Chen et al. 2018) and may advance or delay budburst (Zhang et al. 2007; Fu et al. 2015a, b; Chen et al. 2018). For boreal forests, sufficient chilling is likely to continue (Man et al. 2017) allowing budburst to continue unaffected. However, as climate warms, winter chilling may no longer be sufficient (Morin et al. 2009; Yu et al. 2010; Polgar and Primack 2011; Guo et al. 2015) to meet the relatively high chilling needs of temperate forest species/populations (Hannerz et al 2003; Howe et al. 2003; Guy 2014).

In general, the amount of cumulative forcing needed for budburst decreases rapidly as winter chilling increases, then gradually stabilizes (Cannell and Smith 1983; Hannerz et al. 2003; Man et al. 2017). The rate and timing of chilling completion differ substantially among tree species (Man et al. 2017). To some extent, insufficient chilling may result in additional needs for forcing temperatures and delay budburst, without compromising budburst quality or subsequent growth (Cannell and Smith 1983; Heide 1993; Hannerz et al. 2003; Guak and Neilsen 2013; Harrington and Gould 2015; Man et al. 2017). The chilling–forcing relationship, however, has been examined for only a few tree species, and mostly in European forests (Cannell and Smith 1983; Hänninen 1990; Heide 1993; Hannerz et al. 2003). Compared with budburst timing, which has been the focus of most phenological research on forest trees, limited effort has been directed to understand the effects of insufficient chilling on budburst quality and subsequent growth, which have ecological and economic significance (Polgar and Primack 2011).

The objective of this study was to examine the effects of winter chilling on budburst and growth for six central (Canada) temperate forest tree species: yellow birch (*Betula alleghaniensis*), eastern white pine (*Pinus strobus*), eastern larch (*Larix laricina*), red pine (*Pinus resinosa*), eastern white cedar (*Thuja occidentalis*), and red spruce (*Picea rubens*) following the approach established by Man et al. (2017). These species are major components of Ontario temperate forest ecosystems (Rowe 1972; Burns and Honkala 1990), with significant economic, cultural, and spiritual values (OMNR 1998a, b). Specifically, we are interested in quantifying species-specific chilling and forcing requirements for dormancy release and budburst and more importantly chilling–forcing relationships, i.e., how cumulative forcing responds to different levels of winter chilling. Our goal is to better understand the effects of climate change on bud phenology and growth of Ontario's tree species.

Materials and methods

Experimental seedlings

The seeds of study tree species were collected from multiple open-pollinated trees in seed zones 36 (eastern white pine, red pine, and eastern white cedar), 35 (eastern larch), and 29 (red spruce and yellow birch) (Seed Zones of Ontario "https://www.rrca.on.ca/_files/file/map-tree-seed-zones.pdf?phpMyAdmin=415bcc74a9c69072ce5800d6de86a905") belonging to the Great Lakes-St. Lawrence temperate forests in eastern Ontario (44° 30′–46° 00′ N, and 74° 26′–78° 00′ W). Seeds were sown into 3.8 cm×21 cm SC-10 Super Cell tubes filled with 2:1 peat moss/vermiculite (*v/v*) mixture in late May 2016 and grown in a greenhouse at the Ontario Forest Research Institute in Sault Ste. Marie, Ontario, Canada (46° 30′ N, 84° 18′ W). The greenhouse was programmed to provide 26 °C (day)/18 °C (night) temperatures and a 16-h photoperiod. Seedlings were watered as required and fertilized weekly with 20–8–20 (N–P–K) (Plant Products Co Ltd, Brampton, Ontario, Canada) at 100 ppm N. Beginning early September 2016, seedlings were moved outdoors and fertilization was adjusted to 20–20–20 at 50 ppm N. In early May 2017, the 1-year-old seedlings were transplanted into 4″ square (10 cm sides×15 cm deep) pots filled with 2:1 peat moss/vermiculite (*v/v*) mixture and grown in a greenhouse at the Ontario Forest Research Institute. Seedlings were watered as required and fertilized weekly with 20–8–20 (N–P–K) (Plant Products Co Ltd, Brampton, ON) at 100 ppm N for a month before being moved outdoors in early July. Watering and fertilization continued as required until early September when fertilization was adjusted to 20–20–20 at 50 ppm N and then discontinued in mid-October.

The seedlings were left outdoors for 2 years to undergo natural hardening and dehardening under ambient photoperiod and temperatures. Average seedling height at the outset of forcing experiments in the fall of 2018 was 115 cm for yellow birch, 23 cm for eastern white pine, 127 cm for eastern larch, 31 cm for red pine, 46 cm for eastern white cedar, and 53 cm for red spruce.

Forcing experiments

A series of forcing experiments were carried out to produce different levels of winter chilling and to quantify the corresponding cumulative forcing needed for budburst, and to document effects on subsequent budburst quality and growth. The experiments were conducted in three computer-controlled greenhouses (i.e., three replications) set at 15–20 °C (day)/5–10 °C (night) with natural photoperiod supplemented with high-pressure sodium lamps to 14 h. This temperature and photoperiod regime is typical of late April to late May conditions in northern Ontario, which is when leaf out generally occurs in the study areas (Fig. 1). Batches of seedlings were sequentially moved into the greenhouse from outdoors at about 10-day intervals between October 1st and mid-December and 20-day intervals thereafter to mid-April, which resulted in a time series of 16 forcing experiments for each species (15 in the greenhouses and one outdoors). Seedlings going into these 16 forcing experiments received different levels of winter chilling as they were exposed to outdoor chilling temperatures until being forced to burst bud in the greenhouses. In mid-April, one batch of seedlings (experiment 16) was subjected to additional artificial chilling at 2–4 °C for 15 days to extend the range of what was about average natural chilling during the
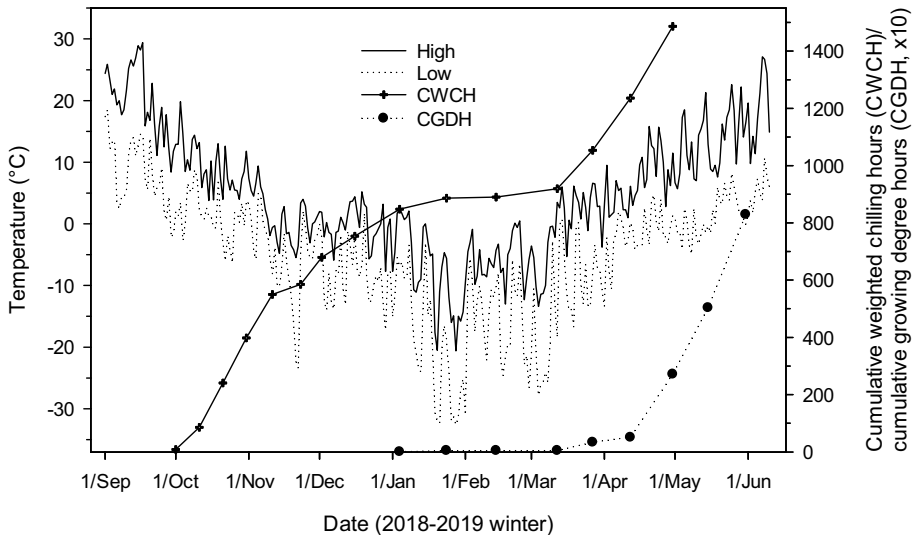
Fig. 1 Outdoor air temperatures (daily high and low), winter chilling (cumulative weighted chilling hours as computed by Sarvas 1974), and spring forcing (cumulative growing degree hours >0 °C since January 1) at the experimental site (Sault Ste. Marie, Ontario, Canada) where the seedlings for forcing experiments were exposed to ambient temperatures from fall 2018 to spring 2019

2018–2019 winter at Sault Ste Marie (Fig. 1; Tables 1, 2). To minimize temperature shock when outdoor temperatures were below −5 °C (early January to late March), seedlings were conditioned at 0–2 °C for 1–3 days before their transfer to greenhouses. In each of the forcing experiments, eight seedlings from each species were placed in each of the three greenhouses (replicates). In all, 384 seedlings per species were used.

Budburst (growth initiation) was assessed daily during the forcing experiments. A bud was considered to have flushed when its scales were broken and new green foliage was clearly visible. Eastern white cedar does not form vegetative buds and the time of growth initiation was determined by the change of shoot length at 1 cm from the tip following the methods by Harrington and Gould (2015). Budburst was considered abnormal for deciduous trees if it started first in lower branches and on stems and for evergreen conifers if bud and needle expansion were constrained. The chilling and forcing accumulations were calculated for individual seedlings based on their timing of budburst (growth initiation). For seedlings that did not flush throughout the experiments, a maximum forcing was calculated from the start of the experiment to May 31 when trees growing outdoors had begun flushing. In late June, all seedlings were moved outdoors to continue growth under natural conditions. Shoot growth on individual seedlings was assessed by measuring the length of the longest shoot 30 days after budburst and again at the end of the growing season (late October), except for eastern larch where apparent new shoot growth did not occur within a month and growth was assessed based on average needle length.

Chilling–forcing relationships

The chilling–forcing relationship was determined for each species using hourly temperature data recorded in the greenhouses and from the Environment Canada weather station at

Table 1 Results of multiple comparisons of cumulative forcing for budburst (growth initiation): (a) differences among forcing experiments within a species, where + and = indicate experimental mean is significantly greater than or statistically insignificant from, respectively, the combined mean of subsequent experiments; and (b) differences between species within an experiment, where ± and = indicate species is statistically smaller/greater than or equal to PR (or LE), respectively

Experiments	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Date	Oct 1	Oct 11	Oct 21	Oct 31	Nov 11	Nov 23	Dec 2	Dec 16	Jan 4	Jan 24	Feb 14	Mar 12	Mar 27	Apr 12	Outd	Apr 12
CWCH	9	86	241	398	550	585	679	754	865	928	946	969	1095	1284	Outd#	1552
(a) Differences among forcing experiments in cumulative forcing required for budburst																
BY	+	+	+	+	+	+	+	+	+	+	=	=	=	=	=	=
PW	+	+	+	+	+	+	+	=	=	=	=	=	=	=	=	=
LE	+	+	+	+	+	+	=	=	=	=	=	=	=	=	=	=
PR	+	+	+	+	+	+	+	+	+	=	=	=	=	=	=	=
CE	+	+	+	+	+	+	+	+	+	=	=	=	=	=	=	=
SR	+	+	+	+	+	+	+	+	+	=	=	=	=	=	=	=
(b) Differences between species																
PR: SR	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
PR: CE	–	–	–	–	–	–	=	=	=	=	=	=	=	=	=	=
PR: LE	+	+	+	+	+	+	+	=	=	=	=	=	=	=	=	=
PR: PW	+	+	+	+	=	+	+	=	=	+	+	=	=	=	=	=
LE: PW	+	+	=	=	=	=	=	=	=	=	=	=	=	=	=	=

Date indicates the time when each forcing experiment began and cumulative weighted chilling hours (CWCH) indicate associated winter chilling. The symbol Outd# refers to chilling accumulation of outdoor (Outd) stored seedlings, which ranged from 1360 to 1486 CWCH due to differences in budburst timing among species

Species abbreviations are: *BY* yellow birch, *PW* eastern white pine, *LE* eastern larch, *PR* red pine, *CE* eastern white cedar, *SR* red spruce

Table 2 Cumulative weighted chilling hours (means ± standard deviation, as computed with Sarvas 1974) and mean winter temperatures (°C, in parentheses) between October 1 and April 30 under three climate scenarios for four locations in the Great Lakes- St. Lawrence temperate forest region in eastern Ontario: Sault Ste. Marie (46° 29′ N, 84° 31′ W), Sudbury (46° 38′ N, 80° 48′ W), North Bay (46° 22′ N, 79° 25′ W), and Ottawa (45° 19′ N, 75° 40′ W)

Time period	Sault Ste. Marie	Sudbury	North Bay	Ottawa
(1) 1950s–1980s	1396 ± 179 (−2.61)	1152 ± 143 (−4.54)	1160 ± 149 (−4.05)	1364 ± 162 (−2.04)
(2) 1990s–2010s	1494 ± 233 (−1.97)	1269 ± 189 (−3.79)	1264 ± 197 (−3.46)	1444 ± 174 (−1.26)
(3) +2 °C	1687 ± 224 (+0.03)	1473 ± 191 (−1.79)	1458 ± 195 (−1.46)	1559 ± 153 (+0.74)

The scenario of +2 °C was obtained from uniform temperature increases of 1990s–2010s, based on recent projections (IPCC 2013)

the Sault Ste. Marie airport (46° 29′ N, 84° 31′ W), about 13 km from the Ontario Forest Research Institute. The rate of chilling was calculated using the Sarvas Chilling Rate Model (Sarvas 1974) which was reformulated by Hänninen (1990) and Kramer (1994). However, the published model parameters produced negative values and were replaced with the following obtained from refitting Sarvas's data

$$CH = \begin{cases} 0.145T + 0.493, & -3.4 < T \leq +3.5 \\ -0.145T + 1.507, & 3.5 < T \leq +10.4 \\ 0 & otherwise \end{cases} \quad (1)$$

where CH is weighted chilling hours, T is the actual temperature imposed on seedlings, and -3.4 °C, 3.5 °C, and 10.4 °C are three threshold values for lower, optimum, and upper limits of effective chilling temperatures. Because of the possible negative effect of high temperatures on chilling effectiveness (Young 1992; Arora et al. 2003), chilling was accumulated from October 1 to the time of transfer to the greenhouses. Similarly, possible chilling in the greenhouses under cooler night temperature (5–10 °C for 10 h) was not considered. For the forcing experiment with outdoor seedlings, chilling was accumulated until the end of April when outdoor daily temperature was generally below 15 °C. As eastern white pine started budburst in late April, its chilling accumulation to the time of budburst was calculated for individual trees.

The cumulative forcing was calculated as temperature sum (cumulative growing degree hours above 0 °C; see Man and Lu 2010) including forcing temperatures in the greenhouses and the outdoor conditions between January 1 and the time seedlings were brought into the greenhouses (Fig. 1).

The relationship between chilling and forcing for budburst was investigated by fitting a 4-parameter sigmoid curve:

$$y = y_0 + \frac{a}{1 + e^{\left(-\frac{x-x_0}{b}\right)}} \quad (2)$$

where y is the cumulative forcing for budburst, x is the total chilling received (i.e., cumulative weighted chilling hours), e is the base of natural logarithm, and y_0, a, x_0, and b are the model parameters. The parameter y_0 is the forcing requirement for budburst, and x_0 and b determine the pattern of chilling completion, i.e., when and how fast chilling completes (Fig. 2). We followed the method by Man et al. (2017) and Hannerz et al. (2003) to determine chilling requirement, which was set as 1.05*y_0, a point slightly before the lowest
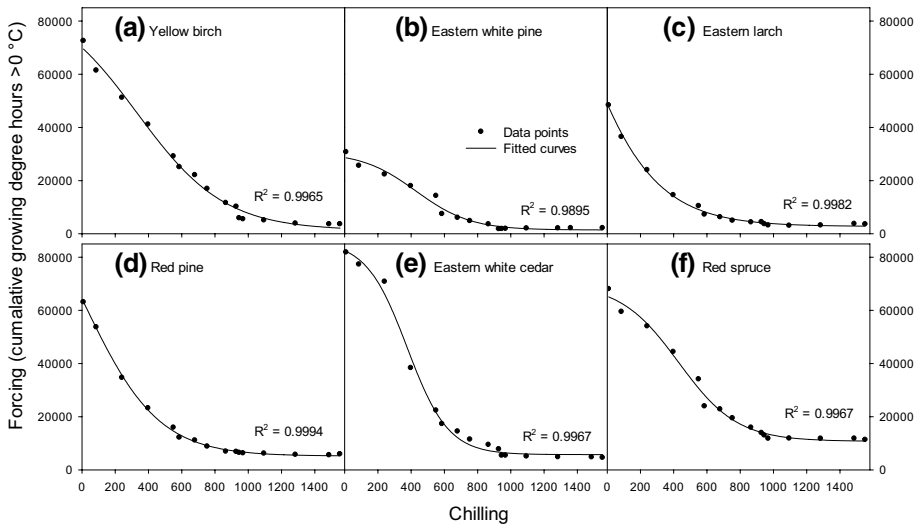
Fig. 2 Sigmoid curves fitted with 16 winter chilling (cumulative weighted chilling hours since October 1) and cumulative forcing for budburst (growth initiation) (cumulative growing degree hours >0 °C) conducted sequentially from October 1 (left, greenhouses) to May (right, experiment 15 for outdoor conditions is second point from the right) for six tree species (**a**–**f**). Experiment 16 (first point from the right) received additional chilling at artificial settings (2–4 °C for 15 days) relative to that of experiment 14 (third point from the right)

value of the fitted curves (Fig. 2). The 3-parameter exponential decay curve used by Cannell and Smith (1983) and Hannerz et al. (2003) is not flexible enough to fit chilling–forcing patterns for different species (Man et al. 2017).

Data analysis

Cumulative forcing for budburst and tissue growth (30 days after budburst and year end) were subjected to a 2-way analysis of variance based on the linear model:

$$y_{ijkl} = \mu + E_i + R_{j(i)} + S_k + ES_{ik} + \varepsilon_{ijkl}$$

where y_{ijkl} is the observation of the l-th seedling of the k-th species tested in the j-th replication of the i-th experiment; μ is the overall mean; E_i is the i-th experiment; $R_{j(i)}$ is the j-th replication within the i-th experiment; S_k is the k-th species; ES_{ik} is the interaction between i-th experiment and k-th species; and ε_{ijkl} is the residual. One-way ANOVA was performed to test differences among tree species in the chilling and forcing requirements determined from chilling–forcing relationships by tree species and replication (individual greenhouses). Multiple contrasts were conducted to examine differences in cumulative forcing for budburst among forcing experiments within a species or among species within an experiment, in chilling and forcing requirements among species, and in tissue growth within a species. The p-values were corrected using Tukey's method in SAS 9.4 (SAS Institute Inc. 2012).

Results

Chilling and forcing requirements

Based on analysis of variance, both forcing experiments (i.e., timing) and tree species significantly affected cumulative forcing needed for budburst ($p < 0.001$ for forcing experiments, species, and experiment by species interaction). The cumulative forcing needed for budburst decreased progressively with experiment start time following sigmoid curves ($R^2 > 0.98$ for all species) (Fig. 2). Among species, the change in cumulative forcing with forcing experiments became insignificant over time, occurring first for eastern larch (by December 2) and last for yellow birch (by February 14) (Table 1). While eastern white pine generally required the least cumulative forcing for budburst, the species requiring the highest cumulative forcing shifted from eastern white cedar for forcing experiments in October to red spruce for forcing experiments after January (Fig. 2; Table 1).

The species ranking for chilling requirements determined from chilling–forcing relationships from highest to lowest was yellow birch, eastern larch, eastern white pine, red pine, red spruce, and eastern white cedar. The species rank for forcing requirements, again from highest to lowest, was red spruce, eastern white cedar, red pine, eastern larch, eastern white pine, and yellow birch (Fig. 2; Table 3).

Effects of insufficient chilling

A minor deficiency in chilling (i.e., between chilling requirements and 1000 cumulative weighted chilling hours or forcing experiments after mid-March) only slightly delayed budburst (greater cumulative forcing) in the six temperate species (Fig. 2; Table 1), without compromising budburst quality and subsequent growth (Figs. 3, 4). The severe reduction in chilling, however, not only substantially increased cumulative forcing and inter-tree variation (Fig. 2; Table 1), but also increased the number of seedlings with abnormally flushed and unflushed buds and reduced subsequent shoot/leaf expansion (Figs. 3, 4). For example, forcing experiments that started before December, when cumulative chilling was <700 weighted chilling hours, produced abnormal budburst including early and erratic budburst in lower branches and on lower stems in yellow birch and eastern larch. In

Table 3 Parameter estimates for a 4-parameter sigmoidal curve (a, b, x_0, and y_0) illustrating the relationship between winter chilling (cumulative weighted chilling hours) and cumulative forcing (cumulative growing degree hours > 0 °C) for the budburst (growth initiation) of the six tree species examined

Species	a	b	x_0	y_0	Ym	Chill
Yellow birch	88,151	− 263	332	1311c	70,012	2225a
Eastern larch	199,142	− 248	− 297	2769c	48,971	1507b
Eastern white pine	29,274	− 165	429	1438c	28,699	1418b
Red pine	113,800	− 221	17	5175b	64,282	1364b
Red spruce	59,227	− 176	430	10771a	65,260	1256bc
Eastern white cedar	80,365	− 124	376	5742b	82,467	1072c

ANOVA statistical difference < 0.001

The parameter Ym is the cumulative forcing with zero chilling, y_0 is the forcing requirement when chilling requirement is met, and Chill is the chilling requirement determined at $1.05 * y_0$
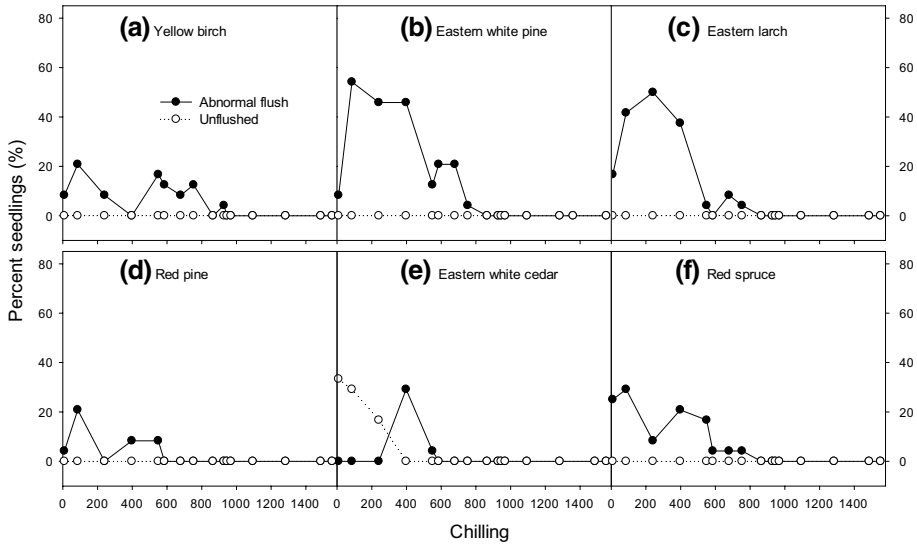
Fig. 3 The relationships between winter chilling (cumulative weighted chilling hours since October 1) and budburst (growth initiation) quality (percent abnormally flushed and unflushed seedlings by May 31) from 16 forcing experiments conducted sequentially from October 1 (left, greenhouses) to May (right, experiment 15 for outdoor conditions is second point from the right) for six tree species (**a–f**). Experiment 16 (first point from the right) received additional chilling at artificial settings (2–4 °C for 15 days) relative to that of experiment 14 (third point from the right)
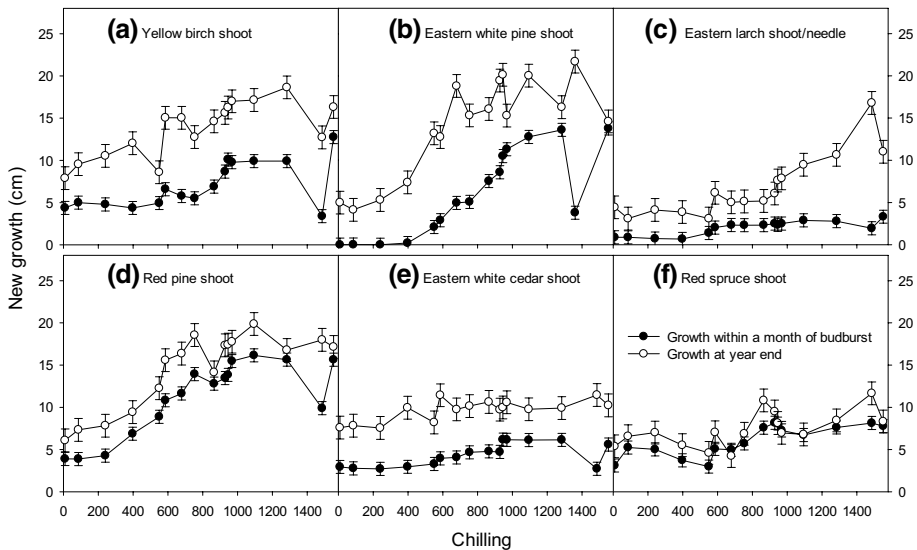
Fig. 4 The relationships between winter chilling (cumulative weighted chilling hours since October 1) and new growth (least square means ± SE) from 16 forcing experiments conducted sequentially from October 1 (left, greenhouses) to May (right, experiment 15 for outdoor conditions is second point from the right) for six tree species (**a–f**). Experiment 16 (first point from the right) received additional chilling at artificial settings (2–4 °C for 15 days) relative to that of experiment 14 (third point from the right). Eastern larch growth was evaluated on needles within a month of budburst and on shoots at year end

evergreen conifer species, extreme chilling deficiency constrained bud expansion, short-ened the length of new needles, and promoted early burst of lateral buds in lower branches. More seriously, some eastern white cedar that received <400 weighted chilling hours did not grow after 7 months of optimal growing conditions in the greenhouse (Fig. 3). All east-ern white cedar eventually grew under outdoor conditions. However, the patterns of new growth observed at 30 days after budburst remained at year end for all species (Fig. 4).

Discussion

Our results indicate that winter chilling is critical for normal budburst and growth of the six Ontario temperate forest tree species studied, which is consistent with other's findings for temperate tree species (Calmé et al. 1995; Arora et al. 2003; Koo et al. 2014; Har-rington and Gould 2015). The estimated chilling requirements were generally in the range of 1000–1500 weighted chilling hours, which occurred after late March (Fig. 1; see also Man et al. (2017) for 2014–2015 winter). These requirements were slightly higher than those found for boreal tree species, which were generally less than 1000 weighted chill-ing hours and were met as early as November (Man et al. 2017). This finding is consistent with the general trend that southern species or populations require more chilling to break dormancy (Hannerz et al 2003; Howe et al. 2003; Guy 2014). Although budburst quality and subsequent growth of the study species are likely not affected by inadequate winter chilling under the current and a likely future climate by the end of this century (Table 2), some effects resulting from minor deficiency in winter chilling, shown as delayed budburst (Fig. 2; Table 1), may occur in some species (Table 3) and years (Table 2). The forcing requirements of the six temperate tree species, however, appeared to be more diverse, and, along with their greater chilling requirements, would result in greater phenological vari-ations among trees and years. Overall, the sigmoid curve provided a better fit for chill-ing–forcing relationships for Ontario's temperate trees species than the exponential decay curve fitted for Ontario's boreal tree species, i.e., trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) based on R^2 and general data trends (Man et al. 2017).

The effects of insufficient chilling are comparable to the findings published for boreal and temperate tree species, i.e., insufficient chilling delays budburst (Cannell and Smith 1983, 1986; Myking and Heide 1995; Heide 2003; Morin et al. 2009; Laube et al. 2014; Fu et al. 2015a, b; Man et al. 2017) but does not cause abnormalities unless chilling hours are too few (Arora et al. 2003; Harrington et al. 2010; Man et al. 2017). Specific information about the six studied species is scarce but generally supports our findings. Berry (1965) showed that eastern white pine broke buds rapidly after 9 weeks at 4.4 °C (1314 weighted chilling hours based on Sarvas Chilling Rate Model), but slowly and abnormally (laterals started earlier than terminals) after 4 and 6 weeks (600–900 weighted chilling hours) and did not break buds after 2 weeks (300 weighted chilling hours), while western white pine (*Pinus monticola*) required at least 14 weeks at 4.4 °C to achieve maximum shoot growth (Steinhoff and Hoff 1972). Similarly, Gustafson (1938) noticed that growth of red pine not exposed to winter chilling was very restricted in the subsequent summer.

As found on boreal trees in Canada (Man et al. 2017), species with low forcing require-ments (early flushing) often have relatively high chilling requirements (i.e., yellow birch, eastern white pine, and eastern larch), contrary to some early suggestions that early flush-ing species tend to have low chilling requirements (Laube et al. 2014; Asse et al. 2018;

Fu et al. 2019). The phenological combination of low chilling with high forcing or high chilling with low forcing helps maximize growth with low risk of frost damage. In contrast, the combination of low chilling with low forcing or high chilling with high forcing is adaptively disadvantageous, resulting in either increasing vulnerability to frost or missed opportunity for growth (Guy 2014; Man et al. 2017). Among the six species in our study, yellow birch had the highest chilling requirement, confirming findings by Man et al. (2017) for boreal tree species that early flushing deciduous species need more chilling than late flushing evergreen conifers and that inadequate winter chilling would be more detrimental to deciduous species. The differences in chilling–forcing relationships among species suggest that the chronological order of budburst among tree species (early vs. late flushing species) may change with level of winter chilling among years and with climate warming (Laube et al. 2014; Roberts et al. 2015).

The Ontario temperate forest region is characterized by long and cold winters where temperatures are generally below the range of effective chilling temperatures from late December to early March (Fig. 1). The increases in temperatures from climate warming increase the contribution to winter chilling from these freezing months (Table 2) (Harrington and Gould 2015; Man et al. 2017). Consequently, future winter chilling will likely be sufficient to meet the requirements of the study species such that budburst would happen earlier with warming temperatures, as has been observed elsewhere (Heide 1993; Chmielewski and Rötzer 2001; Schwartz et al. 2006; Morin et al. 2009; Beaubien and Hamann 2011; Chen et al. 2018). The decelerated or reversed trends of advanced budburst observed in temperate areas with mild winters (Zhang et al. 2007; Morin et al. 2009; Yu et al. 2010; Fu et al. 2015a, b; Asse et al. 2018) are not likely to occur in Ontario temperate forest region.

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